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EFFECTS OF SOIL STRUCTURE ON BURROW CHARACTERISTICS OF FIVE SMALL MAMMAL SPECIES

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ABSTRACT.—Burrows of small mammals can impact a variety of soil processes including organic turnover, aeration, and mineralization rates. The structure of burrows, depth, length, and complexity can influence the extent of the impact burrows have on soil processes. Soil properties, in turn, are thought to affect burrow structure. To increase our understanding of burrow-soil dynamics, we compared maximum depth, total volume, total length, volume:length ratio, and complexity of burrows of five small mammal species with bulk density and soil texture in multiple regression analyses. Burrows of Wyoming ground squirrels (*Spermophilus elegans*) were deeper, longer, and more complex as percentage of silt and clay increased and percentage of sand and bulk density decreased. Average maximum depth of montane vole (*Microtus montanus*) burrows increased as soils became sandier. Length and volume of deer mice (*Peromyscus maniculatus*) burrows increased with increases in bulk density and percentage of clay. Volume, length, and complexity of kangaroo rat (*Dipodomys ordii*) burrows were greater in soils with higher amounts of clay and silt. Townsend's ground squirrel (*Spermophilus townsendii*) burrows did not appear to be affected by the soil properties measured.

Key words: burrow structure, soil, small mammals, bulk density, soil texture, Idaho.

The association between burrowing activity of mammals and the subterranean environment is an interdependent relationship that is receiving increasing attention because of its potential impact on plant community structure (Andersen and MacMahon 1985, Inouye et al. 1987). Burrowing activity of mammals can impact a variety of soil processes including organic matter turnover, inorganic distribution, aeration, and mineralization rates (Abaturov 1972, Chew 1978, Zlotin and Khodashova 1980, Hole 1981, Reichman and Smith 1989). The extent to which burrowing mammals may influence soil processes can depend on the structure (complexity and dimensions) of burrow systems. Deeper burrows increase the depth, and more extensive, convoluted burrows increase the area of influence compared with shallower and simpler systems. Thus, factors that influence burrow structure could ultimately determine the impact a burrow has on soil processes in an area.

Burrow structure varies considerably among species (Reynolds and Wakkinen 1987, Reichman and Smith 1989) and also differs within a species with length of occupation of the burrow or age of occupant (Reichman and Smith 1989). Intraspecific differences in burrow dimensions are also hypothesized to be related to physical properties of soils, e.g., bulk density, texture, etc. (Anderson and Allred 1964, Reynolds and Wakkinen 1987). However, this hypothesis has not been adequately tested. To more clearly understand the dynamic relationship between burrowing mammals and the soil they live in, more information is needed on how soil characteristics impact burrow structure. Assuming soil properties impact burrow structure, we predicted that burrow dimensions within a species should be quantitatively related to changes in measurable soil attributes. The purpose of this research was to test this prediction.

STUDY AREA AND METHODS

To test our prediction, data of Reynolds and Wakkinen (1987) were supplemented with data on burrows from several other soil types. All data came from within two study areas in southeastern Idaho: the Idaho National Engineering Laboratory (INEL), 65 km NNW of Pocatello, Bannock County, and public and private lands near Soda Springs, Caribou County. The INEL, a National Environmental Research Park on the upper Snake River plain, is classified as a cool sagebrush

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(*Artemisia* spp.) desert dominated by sagebrush and grasses (Anderson and Holte 1981). Sample sites near Soda Springs were in three mountain valleys: Wooley Valley, T33N, R43E, Sec. 25; Conda Valley, T8S, R42E, Sec. 23; and Big Canyon, T9S, R43E, Sec. 13. Vegetation at these sites is also a sagebrush-grass mixture.

Multiple regression analysis was used to test the prediction that burrow dimensions within a species are quantitatively related to changes in soil properties. Measurements of each burrow characteristic taken were individually used as the dependent variables; properties of the soils found at corresponding burrow sites were the independent variables. The null hypothesis tested for each analysis was that the multiple regression coefficient was equal to zero.

For each species, burrows were excavated from at least four different subsites, representing a variety of soil types, within the study areas. Subsites were selected based on the presence of burrows in the area. Within the subsites, usually all the burrows were sampled. To quantify soil differences among burrow sites within a species, we measured bulk density (g/cm^3) and soil texture (percent sand, silt, and clay) at approximately 10 cm below the soil surface at burrow locations with the core technique (Blake 1965) and the hydrometer technique (Day 1965), respectively. Soils in the study areas had relatively uniform profiles with little vertical development, so near-surface measurements were considered adequate to classify the soil profile. It is recognized that other soil properties exist and might influence burrowing behavior. However, estimates of density and texture are easily obtained, and other properties such as drainage, structure, and consistency are correlated with these two measurements (Foth 1978).

The measurements we took to quantify the soils are highly correlated and would not be appropriate for use in a regression analysis. To classify soil types based on uncorrelated indices, we used the data on bulk density and soil texture to generate z-score standardized principal component scores (Manly 1990) for each soil sample taken at burrow sites. We then used the first two principal components (soil components) as the uncorrelated independent variables in our regression analyses. All principal component analyses (PCA) were conducted with the Biostat®[3] (Sigma Soft 1430 Shalanwood Land, Placentia, CA 92670) statistical package.

Burrows of five small mammal species were included in this study: Townsend's ground squirrel (*Spermophilus townsendii*), Wyoming ground squirrel (*S. elegans*), deer mouse (*Peromyscus maniculatus*), Ord's kangaroo rat (*Dipodomys ordii*), and montane vole (*Microtus montanus*). Before we examined a burrow system, we determined the species occupying the burrow by making visual observations, snap-trapping, or examining hair and feces near burrow entrances. Little data were available on the age of burrow occupants. Of the animals taken with snap-traps, most were adults. We injected the burrows with polyurethane foam (Felthauser and McInroy 1983), excavated the surrounding soil, and measured the burrow system.

Five measurements were recorded: maximum depth, total length, volume, volume: length ratio, and complexity. Maximum burrow depth to the bottom of the burrow was determined by measuring depth in situ at 10-cm intervals along the total length of the exposed foam casts. Total burrow length was the sum of the main and all side tunnels. After depth and length were recorded, casts were removed and burrow volumes estimated by water displacement (Reynolds and Wakkinen 1987, Reynolds and Laundré 1988). Volume: length ratios were calculated and used as relative indices of burrow diameter to distinguish among different length-diameter ratios, e.g., long-narrow vs. short-wide burrows within a species. The complexity of burrows was calculated as the length of a line connecting the two most distant points of the burrow divided by the burrow's total length. This index is 1.0 for linear burrows and progressively less with increased burrow complexity. This technique was found superior to other "indices of linearity" (Reichman et al. 1982, Cameron et al. 1988) that approached infinity for the short, relatively linear burrow systems found in this study. Additionally, the five burrow characteristics measured were used to generate z-score standardized principal component scores for the burrows of each species. The first principal

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[3] Reference to trade [illegible] endorsement of commercial products.

TABLE 1. Means of measurements (± SD) recorded for burrows examined in this study. The lower portion of the table contains eigenvector coefficients for maximum depth (cm), volume (l), length (m), volume per length (vol/len), and complexity for the first (Z1-b) principal component from the principal component analysis of burrow characteristics. The percent variance (% var) explained by the principal component is also given.

Species	Depth	Volume	Length	Vol / len	Complexity	*n*
Pema[a]	19.2 ± 8.7	1.3 ± 0.9	0.7 ± 0.5	2.1 ± 1.1	0.8 ± 0.2	26
Dior[b]	40.9 ± 19.6	8.3 ± 8.7	2.7 ± 2.3	2.8 ± 0.8	0.6 ± 0.2	17
Mimo[c]	21.1 ± 6.6	1.8 ± 1.3	1.0 ± 0.6	1.8 ± 0.7	0.8 ± 0.2	42
Spto[d]	55.4 ± 36.6	10.2 ± 9.2	2.6 ± 2.5	4.1 ± 1.5	0.7 ± 0.2	19
Spel[e]	64.5 ± 36.2	12.4 ± 18.6	2.0 ± 1.9	5.3 ± 3.2	0.8 ± 0.2	

	First principal component					
Species	Depth	Volume	Length	Vol / len	Complexity	% var
Pema	0.35	0.57	0.55	0.05	−0.51	52.5
Dior	−0.08	−0.56	−0.54	−0.39	0.48	59.3
Mimo	−0.14	−0.68	−0.64	−0.19	0.27	39.2
Spto	−0.39	−0.58	−0.60	0.07	0.39	53.1
Spel	−0.36	−0.54	−0.52	−0.37	0.41	57.6

[a] Deermouse (*Peromyscus maniculatus*)
[b] Kangaroo rat (*Dipodomys ordii*)
[c] Montane vole (*Microtus montanus*)
[d] Townsend's ground squirrel (*Spermophilus townsendii*)
[e] Wyoming ground squirrel (*Spermophilus elegans*)

component score (burrow component, Z1-b) of a burrow was used to characterize a burrow system as a whole. Burrow components within a species were then used as the dependent variable in a multiple regression analysis with the first and second soil components. This analysis would help determine whether the burrow system as a whole was influenced by soil properties.

Ground squirrels construct "shallow" and "deep" burrows (Reynolds and Wakkinen 1987). To test for relationships between shallow or deep systems and soil types, we reanalyzed separately the maximum depth of the two system types for the two ground squirrel species. Shallow burrows for Townsend's ground squirrels were classified as being less than 60 cm deep (Reynolds and Wakkinen 1987). Based on an analysis of frequency distributions of maximum depth found in this study (unpublished data), Wyoming ground squirrel burrows less than 90 cm deep were classified as shallow systems. After the burrows were reclassified as shallow or deep, we found we had sufficient sample sizes to conduct only our regression analyses for shallow burrows.

Statistical comparisons were calculated with Statistics with Finesse® (J. T. Bolding, Box 339, Fayetteville, AR 72702), Biostatistics® (Lincott's Directory, 40 Glen Drive, Mill Valley, CA 94941), or Biostat® (Sigma Soft, 1430 Shalanwood Lane, Placentia, CA 92670) computer packages. All percent data were arcsine transformed before statistical calculations were made. The significance level was $P = .05$, and all reported means are ± standard deviation.

RESULTS

One hundred forty-nine burrow systems were excavated. Means and ranges of measurements recorded are presented in Table 1. Included in Table 1 are eigenvector coefficients for the first principal burrow components (Z1-b) for the five species. Except for montane voles, the first principal components explained 52–59% of the variance of the burrows sampled.

Bulk density and texture of soils at burrow sites varied among the five species and were quite variable within a species (Table 2). The first (Z1-s) and second (Z2-s) principal components of soils from burrow sites explained over 90% of the variance in samples for all five species (Table 2). Eigenvector coefficients for the equations describing the relationship among the soil properties for the first and second principal soil components are also presented in Table 1. For the first principal soil component equation within a species, bulk density and percent sand had the same sign (+ or −), which was opposite the signs for percent silt and clay.

TABLE 2. Means (± SD) and ranges of bulk density (g/cm³) and texture (% sand, % silt, and % clay) of soils from the burrow sites. Texture values are untransformed. The lower portion of the table contains eigenvector coefficients for bulk density (BD) and percentages of sand, silt, and clay for the first (Z1-s) and second (Z2-s) principal components from the principal component analyses (PCA) of burrow site soils. The percent variance (% var) explained by each principal component is also given.

Species	Bulk density	% sand	% silt	% clay	n
Pema[a]	1.36 ± 0.12	34.8 ± 11.5	51.3 ± 9.7	13.2 ± 4.7	15
range	1.12 – 1.50	20.8 – 51.2	31.8 – 62.8	5.5 – 19.8	
Dior[b]	1.28 ± 0.11	45.5 ± 8.9	38.5 ± 6.1	15.5 ± 7.0	11
range	1.15 – 1.48	23.9 – 55.2	25.0 – 46.7	5.6 – 29.8	
Mimo[c]	1.38 ± 0.22	40.8 ± 19.1	47.2 ± 16.4	12.2 ± 5.5	12
range	0.95 – 1.79	15.3 – 71.8	21.2 – 75.0	4.0 – 23.9	
Spto[d]	1.46 ± 0.21	60.3 ± 12.5	32.7 ± 9.3	6.9 ± 4.1	17
range	1.22 – 2.02	37.9 – 73.2	22.7 – 53.9	2.6 – 13.4	
Spel[e]	1.21 ± 0.18	42.5 ± 17.0	45.9 ± 15.0	11.4 ± 4.9	15
range	0.87 – 1.75	9.5 – 67.4	25.3 – 75.9	1.9 – 23.8	

	First principal component					Second principal component				
Species	BD	Sand	Silt	Clay	% var	BD	Sand	Silt	Clay	% var
Pema	+0.01	+0.65	−0.58	−0.49	58.8	+0.82	+0.07	−0.30	+0.48	35.2
Dior	−0.54	−0.61	+0.35	+0.47	62.4	−0.05	+0.69	−0.79	+0.61	28.1
Mimo	−0.49	−0.57	+0.55	+0.36	73.7	+0.48	−0.10	−0.22	+0.84	21.5
Spto	+0.42	+0.55	−0.52	−0.50	78.6	+0.88	−0.29	+0.39	+0.02	13.8
Spel	−0.12	−0.67	+0.64	+0.35	54.5	+0.75	−0.01	−0.21	+0.65	36.7

[a] Deermouse (*Peromyscus maniculatus*)

[b] Kangaroo rat (*Dipodomys ordii*)

[c] Montane vole (*Microtus montanus*)

[d] Townsend's ground squirrel (*Spermophilus townsendii*)

[e] Wyoming ground squirrel (*Spermophilus elegans*)

Of the 28 multiple regression analyses of burrow characteristics with the first and second principal soil components, five were significant (Table 3). Four of the five significant multiple regressions were for characteristics of Wyoming ground squirrel burrows. Coefficients of determination for these four significant multiple regressions ranged from 17% for maximum depth of shallow burrows to 27% for maximum depth of all burrows combined (total depth). For these five significant multiple regressions, the only partial regression coefficient for the first principal soil component that was not significant was for total maximum depth (Table 3). In addition to significant multiple regressions, partial regression coefficients of the first principal soil components were significant for volume per length and complexity. Partial regression coefficients of the second principal soil components were significant only for total maximum depth, shallow maximum depth, and length of burrows (Table 3).

For Wyoming ground squirrels, the multiple regression coefficient for the first principal burrow component (Z1-b) was also significant (Table 3). Of the two independent variables, only the first principal soil component (Z1-s) had a significant partial regression coefficient. There was an inverse relationship between Z1-b and Z1-s, and the regression equation explained 16% of the variability seen in Z1-b (Fig. 1).

The fifth significant multiple regression was for depth of montane vole burrows. The coefficient of determination for this multiple regression was 16% (Table 3). Partial regression coefficients for both independent variables (Z1-s and Z2-s) were significant and negative. The regression equation for depth on Z1-s explained most (10%) of the variability seen in depth of microtus burrows (Fig. 2a). The partial regression coefficient of the first principal soil component was also significant for the volume-length ratios of microtus burrows. The regression coefficient was positive,

TABLE 3. Results of multiple linear regression analyses between burrow characteristics, including the first principal burrow component [Z(1)], and the first two principal components for burrow site soils for the five species examined. Only regressions that were statistically significant are presented. Coefficient of determination (r^2), results of significance tests (F), and probability (P) are given for each multiple regression analysis. Significance values of partial regression coefficients for the principal soil components are also presented. Signs in front of t values indicate direction of the regression relationship.

	Multiple regression			Partial regressions				
				First component		Second component		
	r^2	F	P	t	P	t	P	n
Deer mice								
Volume	.25	2.03	.17	+0.56	.36	+1.94	.04	15
Length	.24	1.72	.22	+0.54	.37	+1.71	.05	14
Z(1)	.38	3.43	.07	+0.32	.50	+2.55	.01	14
Kangaroo rat								
Volume	.31	2.42	.13	+2.08	.03	+0.70	.29	14
Length	.40	3.63	.06	+2.56	.01	+0.85	.35	14
Z(1)	.33	2.21	.16	−1.81	.05	−1.06	.17	12
Townsend's ground squirrel								
Volume	.34	3.04	.08	+0.99	.41	+2.44	.02	15
Wyoming ground squirrel								
Depth								
Total	.27	5.97	.01	−0.87	.37	+3.43	.001	35
Shallow	.17	3.35	.05	+2.02	.02	−1.66	.05	36
Volume	.23	5.67	.01	+3.26	.001	+1.00	.18	40
Length	.19	4.84	.01	+2.15	.02	+2.25	.01	45
Vol/Len	.10	2.04	.14	+1.79	.04	−0.85	.36	40
Complexity	.08	1.61	.21	−1.81	.04	+0.01	.89	45
Z(1)	.18	4.13	.02	−2.73	.005	−0.96	.42	41
Montane voles								
Depth	.16	3.62	.04	−2.08	.02	−1.70	.05	42
Vol/Len	.13	2.67	.08	+2.03	.02	+0.92	.39	39

and the regression equation explained 11% of the variability in the data (Fig 2b).

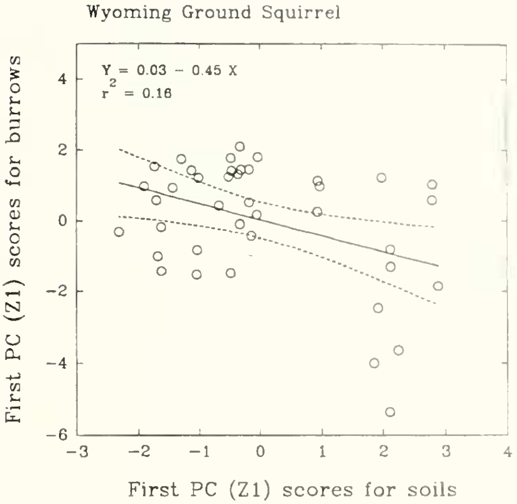
None of the multiple regression coefficients for burrow characteristics were significant for kangaroo rats, deer mice, or Townsend's ground squirrels. However, partial regression coefficients for the first principal soil components were significant and positive for volume and length of kangaroo rat burrows (Table 3). Regression equations explained 27% of the variability in volume (Fig. 3a) and 36% of the variability in length of kangaroo rat burrows (Fig. 3b). Partial regression coefficients for the first principal soil component (Z1-s) and the first principal burrow component (Z1-b) for this species were also significant but negative. The regression equation for Z1-b on Z1-s explained 25% of the variability in the data (Fig. 3c).

For deer mice, partial regression coefficients for the second principal soil component (Z2-s) were significant and positive for volume and length of burrows and for the first principal burrow component (Table 3). Coefficients of determination were 0.23 for volume (Fig. 4a) and 0.22 for length (Fig. 4b). The regression equation for Z1-b on Z2-s explained 38% of the variability in the data (Fig. 4c).

For Townsend's ground squirrels, the only significant partial regression coefficient was for burrow volume on the second principal soil component (Table 3); the regression equation explained 28% of the variability (Fig. 1).

DISCUSSION

Our results indicate that differences in soil properties have different effects on the species of small mammals studied. Townsend's ground squirrels seemed the least affected by soil differences. For this species, only volume was significantly related to the second principal soil component. The second



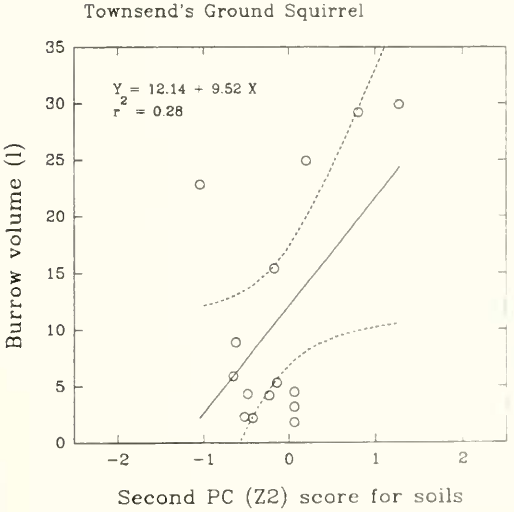


Fig. 1. Regressions, with 95% confidence intervals, of the first principal burrow component scores on the first principal soil component scores for Wyoming ground squirrel burrows, and of burrow volume on the second principal soil component scores for Townsend's ground squirrel burrows. All principal component scores are z-score standardized.

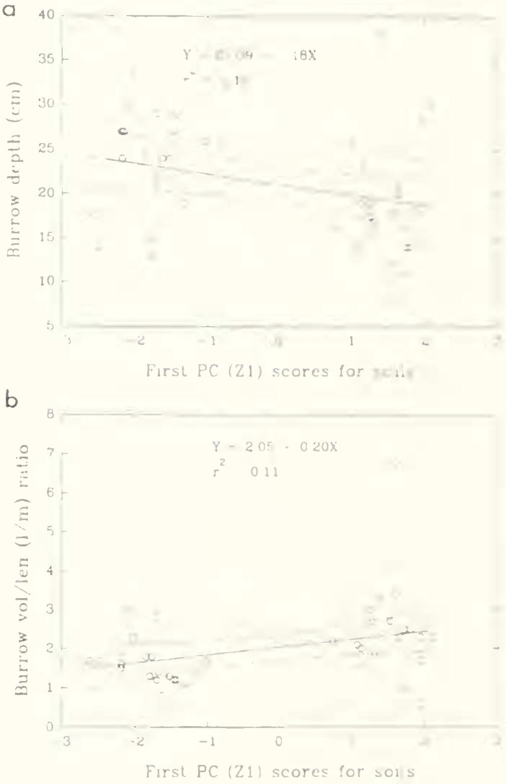


Fig. 2. Regressions, with 95% confidence intervals, of burrow depth (a) and volume per length (vol/len) ratios (b) on the first principal soil component scores for montane vole burrows. All principal component scores are z-score standardized.

principal soil component was influenced positively by bulk density and percent silt and negatively by percent sand (Table 2). Thus, Townsend's ground squirrels constructed larger burrows in the firmer loamy soils. Reynolds and Wakkinen (1987) found significant regression relationships for this species among soil texture components and burrow depth, length, and volume. However, they used individual soil separates (percent sand, silt, and clay) in their analysis. As percent sand, silt, and clay are highly correlated, their use could bias the results of a regression analysis and account for the different findings between the two studies.

For kangaroo rats, burrow length and volume seemed directly influenced by the percentage of silt and clay in the soil. There was a significant negative regression of the first principal burrow component (Z1-b) on the first principal soil component (Z1-s) (Table 3). The magnitude of the first principal soil component is directly related to percent silt and percent clay and inversely related to percent sand and bulk density (Table 2). The first principal burrow component is inversely related to all burrow measurements except complexity (Table 1). However, a decrease in the complexity index indicates more complex burrows. Of the measurements, burrow depth

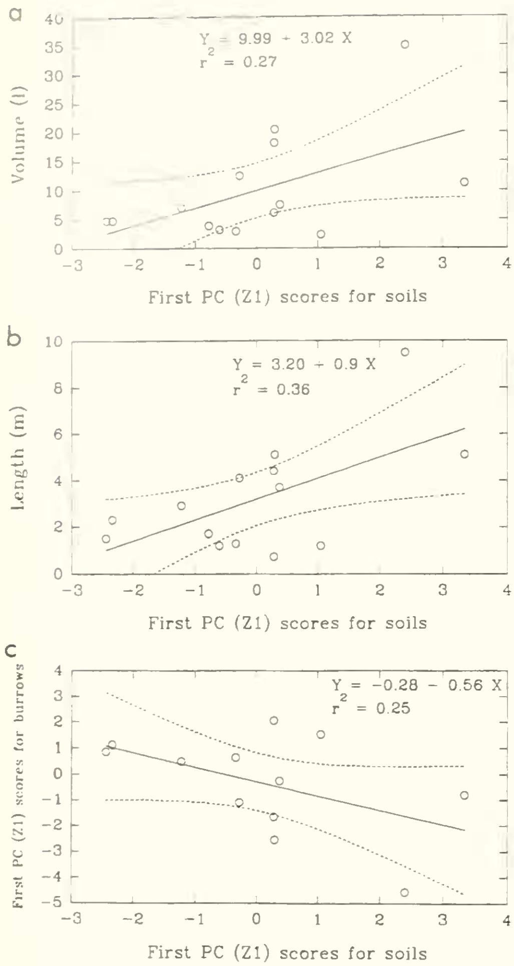


Fig. 3. Regressions, with 95% confidence intervals, of volume (a), length (b), and first principal burrow component scores (c) on the first principal soil component scores for kangaroo rat burrows. All principal component scores are z-score standardized.

contributes little. Consequently, as the percentages of silt and clay increase (high Z1-s), burrows do not become much deeper but they do become longer and more complex (low complexity index), resulting in greater volumes of soil being removed (low Z1-b). This interpretation is supported by the significant and positive partial regression coefficients found for burrow volume and length with the first principal soil component (Table 3). Reynolds and Wakkinen (1987) did not find any significant relationship between burrow characteristics and soil texture for this species. Again, differences in data analysis likely accounted for their different findings.

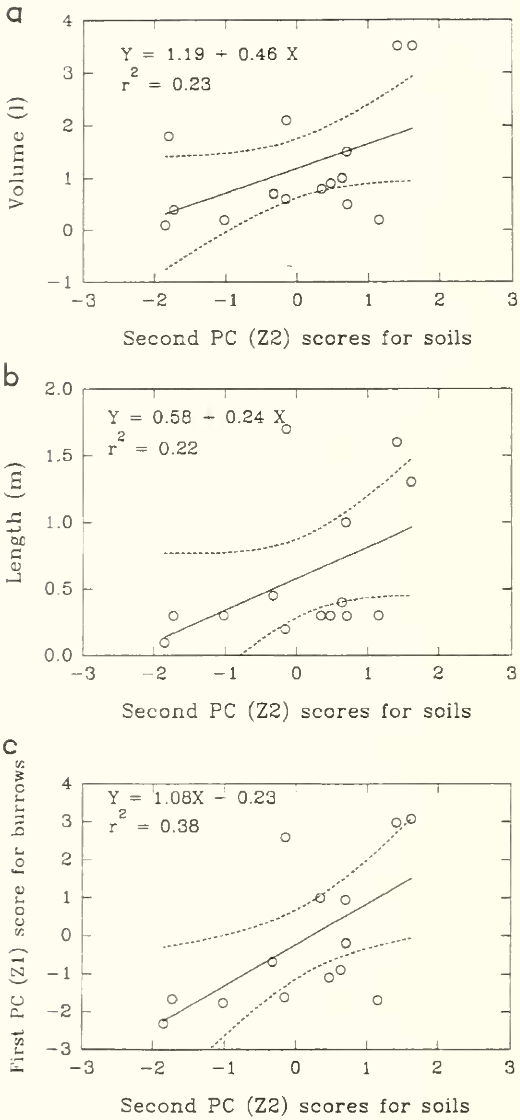


Fig. 4. Regressions, with 95% confidence intervals, of volume (a), length (b), and first principal burrow component scores (c) on the second principal soil component scores for deer mice burrows. All principal component scores are z-score standardized.

Several deer mice burrow characteristics, including the first principal burrow component, seemed to be influenced by soil properties as expressed by the second rather than the first principal soil component. For deer mice, the magnitude of the second principal soil component (Z2-s) increases as percent clay and bulk density increase or percent silt decreases; percent sand does not appear to influence this second soil component (Table 2). Relative to the first principal burrow component (Z1-b), all burrow measurements except complexity increased with higher component scores (Table 1). However, volume/length measurements did not contribute substantially to the score. Consequently, deer mice constructed deeper, longer, and more complex burrows (high Z1-b) in soils with higher bulk densities and percent clay (high Z2-s).

Burrowing behaviors of Wyoming ground squirrels seemed the most affected by differences in soil properties. Wyoming ground squirrel burrows had the most significant regression coefficients between characteristics and principal soil components. The first principal soil component (Z1-s) increased with increasing silt and clay and decreased with increasing bulk density and sand (Table 2). The first principal burrow component (Z1-b) was negatively related to all burrow properties except complexity (Table 1). As percent silt and clay increase (high Z1-s), all burrow characteristics increased (low Z1-b).

For montane voles, only depth and volume/length ratios of their burrows seemed influenced by soil properties. The first principal soil component was positively influenced by percent silt and clay and negatively related to percent sand and bulk density (Table 2). The relationship between depth and the first principal soil component was negative. Conversely, the volume/length ratio was directly related to the first principal soil component. Consequently, voles constructed deeper but narrower burrows in sandier but firmer soils.

In summary, five measurements supported the prediction that burrow characteristics are affected by soil properties. Most of these five characteristics were of Wyoming ground squirrel burrows, and we conclude that the burrows of this species are influenced in a predictable manner by the soil properties measured. Ten of the remaining burrow measurements were also significantly influenced by soil properties as described by individual principal soil components. We conclude that the remaining burrow measurements were not affected by soil attributes. Variability of these burrow properties is likely influenced by other, yet to be determined, factors such as length of occupancy or age and sex of occupant. To investigate the influence these factors may have on burrow structure and further delineate the impact of soil properties, we suggest that controlled experiments be conducted.

Our results suggest that soil characteristics of an area can affect various burrow dimensions in a predictive manner for the five small mammal species we studied. Soil effects on burrow structure could, in turn, influence the soil processes of that area. A difference in maximum depth of burrows changes the location of the reservoir of nutrients for recycling, increases the depth of soil aeration, and, especially in arid and semiarid areas, alters shallow subsurface water recharge patterns. Differences in volume, length, volume/length ratio, and complexity probably have a greater impact on the magnitude rather than the direction of the influence of a burrow on soil properties. For burrows of the same species with the same maximum depth, longer, larger, or more complex burrows within a given area would result in more surface soil deposition from, more aeration of, and more water infiltration to a given profile depth than shorter, smaller, or simpler burrows.

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